

ADDITIONS TO THE REVISED LIST OF PRESERVED MATERIAL OF THE EXTINCT CAPE COLONY QUAGGA AND NOTES ON THE RELATIONSHIP AND DISTRIBUTION OF SOUTHERN PLAINS ZEBRAS

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(With 9 figures)

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ABSTRACT

Previously unpublished photographs and data of two mounted skins of the extinct quagga (*Equus quagga quagga*) and a further relic are added to the list of preserved material. Photographs of the destroyed Königsberg quagga are reproduced.

Examination of plains zebra (*Equus 'burchelli'*) skins from southern Africa and comparison with the true Burchell's zebra (*Equus 'burchelli burchelli'*) and the quagga (*Equus quagga quagga*) suggest that all belong to one species (*Equus quagga*) and are forms which are dominant in certain areas within the continuous distribution, rather than subspecies. In addition, the true Burchell's zebra is considered to be still extant in Zululand and possibly Swaziland, if the generally accepted but vague range of that 'subspecies' is ignored.

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INTRODUCTION

Since the publication of the revised list of preserved material of the quagga (*Equus quagga quagga*) a photograph of and additional data on the quagga at the Zoological Museum, State University at Kazan, Soviet Union, have now been obtained. In addition, a mounted quagga has been discovered at the Muséum d'Histoire Naturelle Lyon, France, and a mounted foot at the Royal Albert Memorial Museum at Exeter, England. These new data are presented in accordance with the method followed by Rau (1974). The photographs included in the description of the Königsberg quagga (Hilzheimer 1930), which was destroyed at the end of the Second World War, are reproduced to complete the illustrations of mounted skins which existed into this century.

In a monograph Antonius (1951), a world authority on zebras, included the quagga and the Burchell's zebras in the single species *Equus quagga*, as had been done earlier (Pocock 1904; St Leger 1932). This view is supported by Rzasnicki (1951), Mohr (1964) and Klingel (1969, 1972) amongst others. There is, however, a second school of thought which divides them into two species, *Equus quagga* and *Equus burchelli* (Ansell 1971). As the present study has revealed that there is no definite division between the quagga and Burchell's zebras, the former view is supported.

ADDITIONAL MATERIAL

KAZAN—MOUNTED SKIN

Fig. 1

Catalogue number: 109

Sex: female

Locality: unknown

Date of acquisition: 1843

Remarks on acquisition: bought in Hamburg from a Mr Brandt by Professor Eversman for the Zoological Museum of Kazan University



Fig. 1. Kazan quagga.

History of mount: bought as mounted specimen in bad condition and remounted; a second remounting ('restoring') was performed in 1969 by M. A. Zaslavski in Leningrad, U.S.S.R.

Description of striking features: face clearly striped; shadow-stripes on neck; posterior part of feet (fetlock-hoof) dark; the photograph seems to show faint striping on buttock

<i>Measurements:</i> head-body	2,36 m*	(2,42 m)*
tail	0,54 m	(0,53 m)
ear	0,14 m	(0,17 m)
hind foot	0,56 m	(0,54 m)
shoulder height	1,29 m	(1,28 m)

State of preservation: appears to be good

Further material of same individual: none

Remarks: exhibited open in gallery

References: none known

LYON—MOUNTED SKIN

Fig. 2

Catalogue number: 6102

Sex: female

Locality: Kaffraria, South Africa

Date of acquisition: unknown

Remarks on acquisition: none

History of mount: appears to be the original mount

Description of striking features: face not clearly striped

<i>Measurements:</i> head-body	2,10 m
tail	0,40 m
ear	0,17 m
hind foot	0,50 m
shoulder height	1,15 m

State of preservation: fair

Further material of same individual: none

Remarks: exhibited; specimen not mentioned in previous literature; V. Eisenmann of the Muséum d'Histoire Naturelle, Paris, discovered this specimen early in 1975 and kindly informed the author

References: M. Philippe, 'La zoologie au Muséum d'Histoire Naturelle de Lyon' (in preparation)

* Measurements received through two intermediaries are not identical.



Fig. 2. Lyon quagga.

EXETER—FOOT TROPHY

Fig. 3

Catalogue number: A758

Locality: Bontebok Flats, British Kaffraria, South Africa (between present Cathcart and Queenstown)

Date of acquisition: after 1869

Remarks on acquisition: from the collection of W. S. M. D'Urban, first curator of Exeter Museum

Measurements (hoof only):

anterior height	6,0 cm
width	6,7 cm
length	8,4 cm

References: Howes & Bamber (1970)

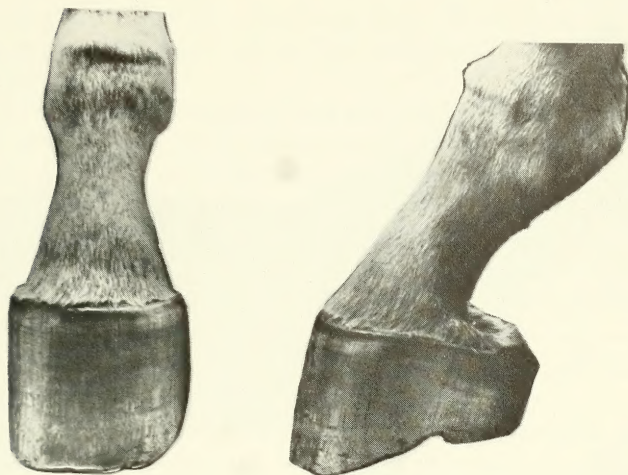


Fig. 3. Exeter quagga foot; anterior and lateral views.

KÖNIGSBERG QUAGGA

Fig. 4

The Königsberg quagga was destroyed at the end of the Second World War when Schloss Waldhof, about 20 km from Königsberg, where museum specimens had been taken for safe-keeping, was shelled and completely destroyed by fire (pers. comm. Prof. Dr O. Koehler (1972), director of the Königsberg Museum until 1945).

The preserved material of *Equus quagga quagga*, including the above specimens, now consists of:

- skins—23, plus 1 mounted head and neck
- complete skeletons—7
- skulls—20, including 7 from complete skeletons; at least 3 of the mounted skins appear to contain skulls
- loose skeletal parts—2 sets of foot bones; upper and lower incisivae in portion of jaws
- other—dried connective tissue, flesh, etc., removed from skin; nasal cartilages and palate removed from skull (in alcohol) (Rau 1974: 58)

NOTES ON BURCHELL'S ZEBRA AND QUAGGA

During February to October 1977 approximately 400 privately owned skins of plains zebra *Equus quagga (burchelli)* and mountain zebra *Equus zebra hartmannae* were processed at a Cape Town tannery and examined by the author. These originated from many different localities in southern Africa. Skins of 113 plains zebras were photographed, the initial 88 non-selectively and



Fig. 4. Königsberg quagga (destroyed), adapted from Hilzheimer (1930).

the remaining 25 selectively. The proportion of the two species processed during a two-month period (February and March) was 88 plains zebra: 62 mountain zebra.

A great number of 'subspecies' and even 'species' of plains zebra have been described. In bestowing names to the many variations, the stripe pattern has been the principal, and often the only, character considered (Ansell 1971). This is certainly true in the case of the 'subspecies' *burchelli*.

The diagnostic characteristics of the true Burchell's zebra *Equus quagga burchelli* are usually given as follows: whitish, unstriped legs except occasionally some traces of stripes on the hocks (Pocock (1897: 52) accepts some stripes on the 'knees' as well); basic colour of dorsal parts white to ochre and brownish; interspaces with shadow-stripes, which may be broad and intense, or less conspicuous; body-stripes not meeting the ventral midline.

Equus quagga antiquorum is defined by the striping extending on to the legs to at least the 'knees' and hocks, but sometimes to the pasterns.

Equus quagga burchelli (*E. burchelli burchelli*) is one of the few still recognized as a valid subspecies. The accepted distributional range of this subspecies included the Orange Free State, the north-eastern Cape Province, southern Botswana and the south-western Transvaal. As zebras no longer occur in these regions, other than reintroduced specimens, the true Burchell's zebra is usually considered to have been extinct since about 1910.

The locality of the type specimen on which Gray (1825) based the description of the subspecies is between Campbell and the Vaal River. The specimen figured as *Equus quagga burchelli* by Antonius (1951, fig. 22) originated from British Bechuanaland (Botswana) and lived at Hagenbeck's Tierpark, Germany, during 1907-9. However, most preserved specimens of this subspecies lack locality data, as do those individuals that lived at menageries or zoos and are known from illustrations and/or descriptions.

It appears, therefore, that the accepted range is based on old reports rather than collected material, and that the true range is not known. Indeed, different opinions as to the range of *Equus quagga burchelli* have been expressed. Matschie (1894) has included Zululand while Shortridge (1934) and Eloff (1967) extend the range to Great Namaqualand (South West Africa). The concept of the range of a subspecies within the continuous distribution of a species is open to question, especially in the case of fast-moving and migrating animals such as the plains zebra. With regard to zebra distribution, Tegetmeier & Sutherland (1895) wrote: 'Disputing, therefore, as to whether two closely allied animals are specifically or sub-specifically distinct is almost a waste of words. We know that a species spread over a wide area will change according to the conditions of life, until at last the two extremes are so diverse as to be regarded as distinct species, but no one can say where one species ends and the other begins, for they merge gradually into each other.'

The uncertainty about the former range of the subspecies *Equus quagga burchelli* has been aggravated by the indiscriminate use of the names 'quagga'

and 'Burchell's zebra', and by the difficulty in distinguishing between those two forms as well as between the true Burchell's zebra and its northern relatives.

Accurate assessment of old documents is, therefore, practically impossible. Pocock (1897: 42) wrote 13 years before the alleged extinction of *Equus quagga burchelli*: '... and on account of the general application of the term *Burchelli* to any or all of its subspecies, we are in ignorance of the exact area that it now occupies in S. Africa.'

If all the mounted zebra specimens preserved in museums had precise locality data, there would be in all probability *antiquorum*-types from the *burchelli* 'range' and vice versa. Since most older mounted zebras do not, however, have conclusive locality data, it is accepted that apparent *burchelli* specimens originate from the accepted *burchelli* range while *antiquorum* patterned specimens are thought to be from further north. Since the plains zebra has a continuous distribution, recent interferences by man excepted, within which certain forms or variations predominate in certain areas, it follows that, in intergradational areas between two forms, the one form will gradually decrease in percentage of total numbers as the area of the next form is approached.

Despite the fact that for most of the preserved or known plains zebra specimens, which conform basically to the description of *Equus quagga burchelli*, the place of origin is not known, they are accepted as belonging to that subspecies, as is shown in the figures by Cabrera (1936) (Fig. 5) and Antonius (1951).

The subspecies *Equus quagga antiquorum* is presently considered to include all the extant southern forms of the plains zebra, ranging from southern Angola and (historical) Damaraland through Botswana and Transvaal to Zululand. Consequently, individual variation within *antiquorum* is considerable (Fig. 6). Eloff (1967) stated that the three subspecies *antiquorum*, *chapmani* and *wahlbergi* occur together in Zululand. Antonius (1951) had observed that in Damara zebra and especially in Wahlberg zebra *burchelli*-like individuals do occur.

However, such individuals originate from outside the presumed range of the true Burchell's zebra and are consequently not accepted as such. Nevertheless, some authors are cautious. Cabrera (1936: 94), while saying that the subspecies 'appears to be extinct', also states, 'in fact, I regard as typical *burchelli* all members of the species having all four legs white from the elbow and the stifle joint, except for the occasional presence of a few short markings across the hocks, and with the thighs free of complete and well-defined dark stripes behind the stifle stripe'. Dorst & Dandelot (1970) list the subspecies *burchelli* as 'probably extinct'.

Amongst the extremely variable skins (many with numerous small, light dots in stripes and shadow-stripes) examined at the tannery, were several specimens from a Zululand game farm with a surprising combination of light basic colour and few and/or weak shadow-stripes and considerable stripe reduction (Fig. 7A). It is generally believed that the change in coloration of plains zebras to the south of their distributional range is achieved by stripe-

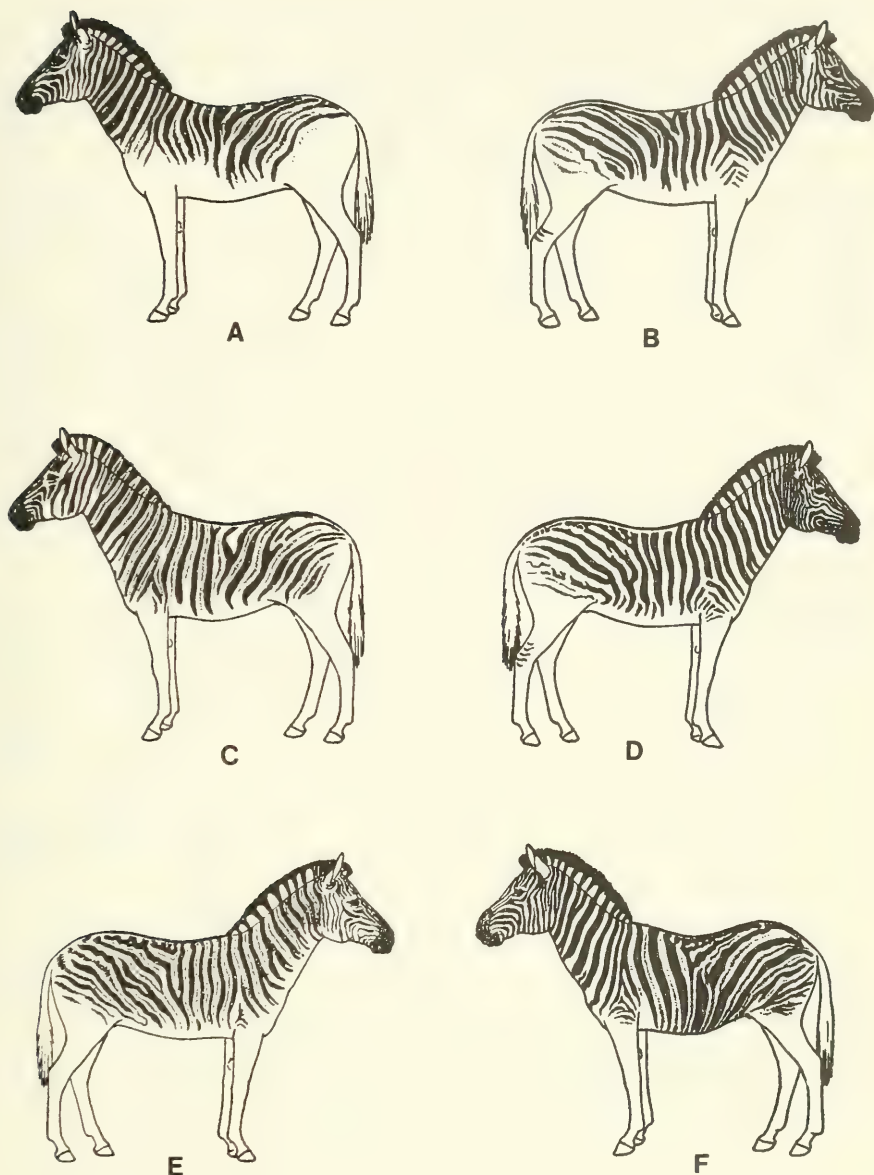


Fig. 5. Examples of true Burchell's zebra, *Equus quagga burchelli*, shown in standardized outline. A. Type of '*Equus burchelli paucistriatus*' Hilzheimer, 1912, at Mainz Museum. B. Animal that lived at Jardin des Plantes, Paris, 1826. C. Type of subspecies from Little Klibbolikhonnifontein, British Museum (Natural History) (destroyed). D-E. Animals that lived at Knowsly Park, about 1845. F. Animal that lived at Zoological Garden, Dresden. (Adapted from Cabrera (1936).)

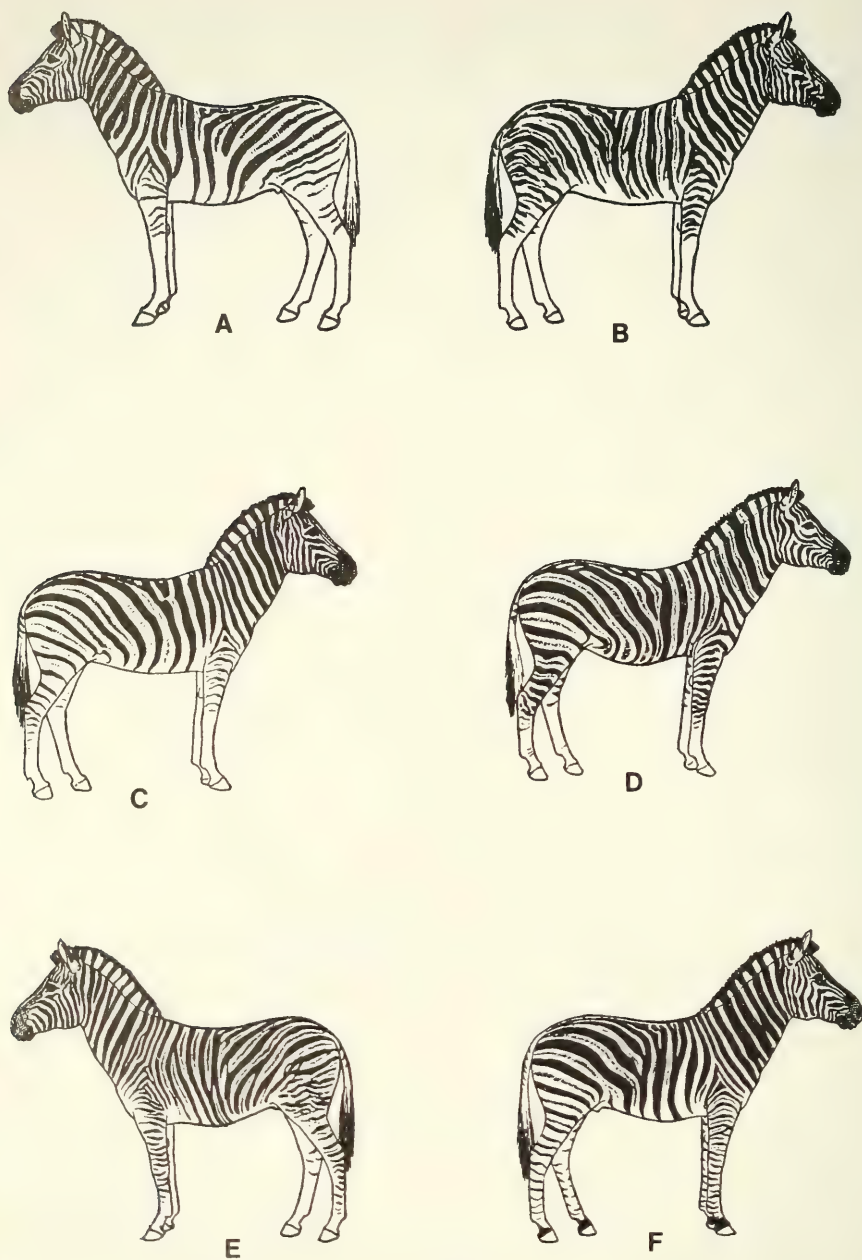


Fig. 6. Examples of *Equus quagga antiquorum*, shown in standardized outline. A. From Rietfontein West, Munich Museum. B. Type of subspecies from Angola (Smith 1841). C. From eastern Transvaal. D. From west of Lake Ngami. E. From Zululand. F. From eastern Transvaal. (Adapted from Cabrera (1936).)

reduction and the darkening of basic colour and the occurrence of shadow-stripes. However, the above specimens indicate that these processes do not necessarily occur together. Indeed, there are specimens from other areas which, in spite of more extensive striping, display dark basic colour (Fig. 8A), some with numerous strong shadow-stripes (sometimes three in one interspace). From the Zululand skins (Fig. 7) and additional photographs it appears that stripe-reduction is the dominant feature in this eastern population, while to the west on the interior plateau the darkening in both basic colour and through shadow-stripes is more pronounced.

In terms of stripe reduction these Zululand skins certainly do not fit into the concept of *Equus quagga antiquorum* (Fig. 6), but they do agree with the description of *Equus quagga burchelli*. Indeed, a few are less striped than some of the *burchelli* specimens figured by Cabrera (1936) (Fig. 5) and others. It appears, therefore, that *Equus quagga burchelli* is, in fact, not extinct but still survives in Zululand (and possibly Swaziland), and that its range does extend eastward into Zululand, as Matschie (1894) stated. (The 'myriads of Quaggas' which Chapman (1868, cited in Antonius 1951: 96) encountered in the extreme north-eastern Orange Free State could thus have been true *burchelli*, and not as Antonius (1951: 96) considered, Wahlberg zebra.) Otherwise the subspecies *burchelli* would have to be considered as part of the *antiquorum* complex, a thought similarly expressed by Rzasnicki (1951) and Roberts (1951), cited in Ansell (1971). The only other alternative would be not to recognize such individuals (Figs 7B–D, 9B, D) as members of the subspecies *burchelli*. However, had they been old mounted specimens, they would be regarded as true Burchell's zebras.

It must be noted that the farm where these specimens had been shot is a hunting farm which was originally stocked with 300 zebras from Hluhluwe Game Reserve, and that hunters select the most striped specimens (C. Tinley, pers. comm.). Selective breeding is thus exercised unintentionally and this might have 're-created' *burchelli*, although similar specimens do occur in Hluhluwe and Umfolozi Game Reserves, the only area in Zululand where the original zebra population has not been interfered with through reintroductions (P. M. Brooks, pers. comm.).

Zululand undoubtedly is an inter-gradational area between the two forms *burchelli* and *antiquorum*. Observations made during a recent visit to that area and Swaziland suggest that the percentage of *burchelli* types may be as high as 15 in Zululand, although P. M. Brooks, biologist at Hluhluwe, estimates it to be 5–10 per cent (pers. comm.).

The north-eastern and eastern parts of Swaziland also retain an endemic population of plains zebra (T. E. Reilly, pers. comm.). There is no geographic barrier between Zululand and the Swaziland lowveld, and it is not surprising that some of the zebras observed there fit or approach the description of *Equus quagga burchelli*, though the percentage of such specimens must be expected to be lower than further south.

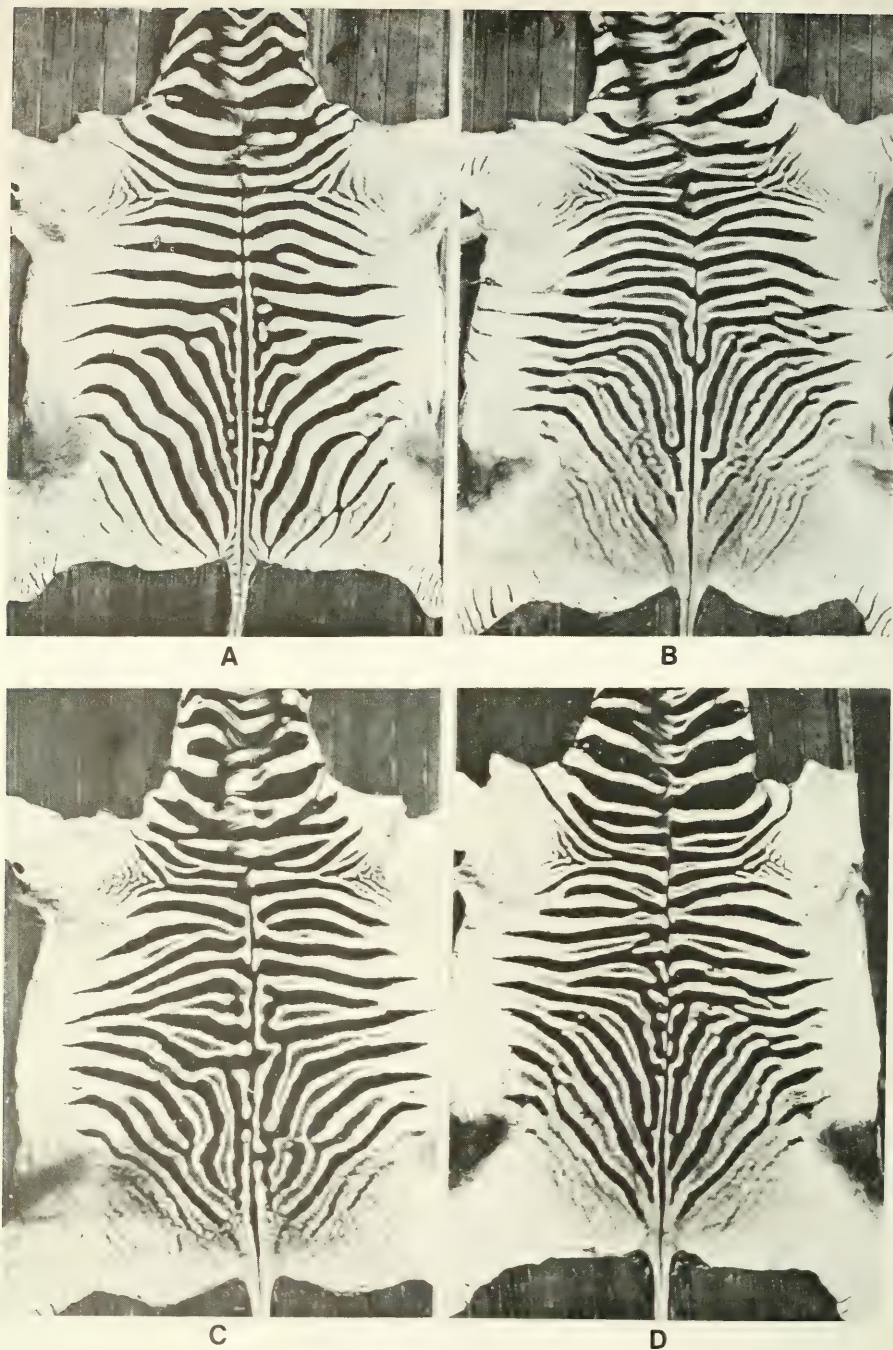


Fig. 7. Skins of plains zebras from Zululand, 1977. A. Note stripe-reduction, few shadow-stripes. B-D. Note shadow-stripes on neck and stripe-reduction. (B now at South African Museum, ZM38819.)



Fig. 8. Skins of plains zebras from southern Africa. A. Precise locality unknown; note dark basic colour of upper parts compared to lower leg. B. Precise locality unknown; note numerous shadow-stripes and extensive striping. C. From game farm in Zululand; note dark basic colour of upper parts. D. From southern Kaokoveld, South West Africa; note little contact between body-stripes and dorsal midline.

Despite the uncertainty whether the 'quaggas' of old reports were, indeed, the true quagga, *Equus quagga quagga*, the northern boundary of its range is usually considered to have been formed roughly by the Orange and Vaal rivers. The eastern limit might have been about the boundary between the Orange Free State and Natal (Grout, cited in Shortridge 1934: 402). It is also generally accepted that the ranges of quagga and true Burchell's zebra overlapped in the Orange Free State (Antonius 1951; Liebenberg 1964; Ansell 1971).

Antonius (1951) was of the opinion that the quagga, being essentially a form adapted to the Karoo and possibly the most distinct of all the plains zebra subspecies, expanded its range secondarily in a northerly direction and met and overlapped along a broad front with the southward expanding Burchell's zebra. He obviously did not believe in reports about the social and reproductive separation of the two forms, since he considered one of the preserved quagga specimens (the more striped specimen of '*Equus burchelli paucistriatus*' at Mainz (Fig. 9A and Rau 1974, fig. 13) as a possible cross between the two forms (Antonius 1951: 26).

It is difficult to accept that separate herds of the two forms existed in the same locality. Even if they did represent separate species, as some are inclined to believe, herds formed by members of both must be expected, since this is known to occur in extant zebra species where their ranges overlap. For example, *Equus zebra hartmannae* overlaps with *Equus quagga antiquorum* in South West Africa (Antonius 1951: 82) and *Equus grevyi* forms mixed herds with *Equus quagga boehmi* in Kenya (Antonius 1951: 82; Bartlett 1963). Even true quaggas were seen together with the Cape mountain zebra at Geelbeckfontein, at the southern limit of the Karoo, by Barrow (1801, cited in Antonius 1951: 82).

As shown previously (Rau 1974) the quagga and the true Burchell's zebra approach one another in basic colour and in stripe reduction, so much so that some of the preserved specimens (e.g. Rau 1974, fig. 12 right) have variously been regarded as one or other of the two. Furthermore, some of the characteristics previously considered to be typical of the quagga (Rau 1974) have been observed in the skins at the Cape Town tannery and in a specimen from Kruger National Park. These characteristics include narrow interspaces (Smuts 1974, fig. 1.4.5), dorsal midline being flanked by a light band on either side, and body-stripes not in contact with dorsal midline except sometimes via narrow bridges (Fig. 8D).

Antonius (1951: 29) has already pointed out that the quagga had reddish dark-brown stripes which, especially on the body, merge into the reddish basic colour. It has previously been explained why the coloration of the quagga has been incorrectly interpreted as light stripes on a dark background (Rau 1974: 43). Careful examination reveals beyond all doubt that the quagga, like all the other plains zebras, is dark-striped and that the interspaces darken progressively from the shoulder in a posterior direction until they become equal in tone with stripes and shadow-stripes to produce the 'uniform' posterior portion. In other southern plains zebras the interspaces are also lightest on head and neck. Ansell (1971: 5)

and others are wrong in defining the striping in the quagga as 'whitish on dark background'.

Since identification is therefore complex, and since it is impossible to observe the stripe pattern of each individual when looking at a herd, the alleged recognition of separate herds of quaggas and Burchell's zebras in the same locality must be treated with suspicion.

The grouping of plains zebras into subspecies is thus somewhat vague, or, as it is expressed by Ansell (1971) 'has never been satisfactory'. In an attempt to sort out this confusion, Pocock (1897) pointed out that throughout the distribution area of the plains zebra 'intermediate types' do exist between particular forms which prevail in particular localities. In addition, as mentioned earlier, typical representatives of the two forms occur in intergradational areas, the closer to the area of the one form the lower the percentage of the other form.

The high degree of variability, both between geographically distant populations and within one herd, has been attributed by Antonius (1951) to the process of eliminating the contrasting stripe-pattern. It should be noted that Antonius's 'Rückbildung der Bein- und Rumpfstreifung' has been misinterpreted by Eloff (1966, 1967) as being a sign of genetic pauperization.

As shown above, the gradual change from one form to another in plains zebras appears to include, at least in exterior characteristics, the 'separation' into *Equus quagga* and *Equus burchelli*. Relatively few skulls of the true quagga are available and some of these lack sufficient data to establish their authenticity. The fact that some skulls may have been obtained by breaking up an old stuffed quagga skin (as has happened at Berlin, where the skull was later identified as that of *Equus caballus* (Antonius 1951: 35)) is no guarantee of their identity as *Equus quagga quagga*.

However, some zoologists believe that there are specific morphological differences between skulls of the quagga and the plains (Burchell's) zebra (e.g. Cooke 1950; Lundholm 1951; Gentry 1975; V. Eisenmann, pers. comm.). The recent study by V. Eisenmann (pers. comm.) has shown that in some skull characters there is a cline from northern to southern plains zebras. In other words, in some respects at least skulls of southern plains zebras approach those of the quagga more closely than do northern forms. This conforms to the well-documented cline in colour and stripe-pattern.

To conclude, it would appear that the Burchell's zebras and the quagga should be regarded as one species, *Equus quagga*. Furthermore, since the grouping into subspecies, either by appearance or by distribution, is not clear-cut in the case of the plains zebras, it might be preferable to refer them to forms, types or variations prevailing in certain areas, rather than to subspecies.

REINTRODUCTIONS OF ZEBRAS

The reintroduction of animal species into areas where natural populations have been exterminated is increasingly common. There are, however, problems with this practice, some of which have been discussed by Greig (1977).

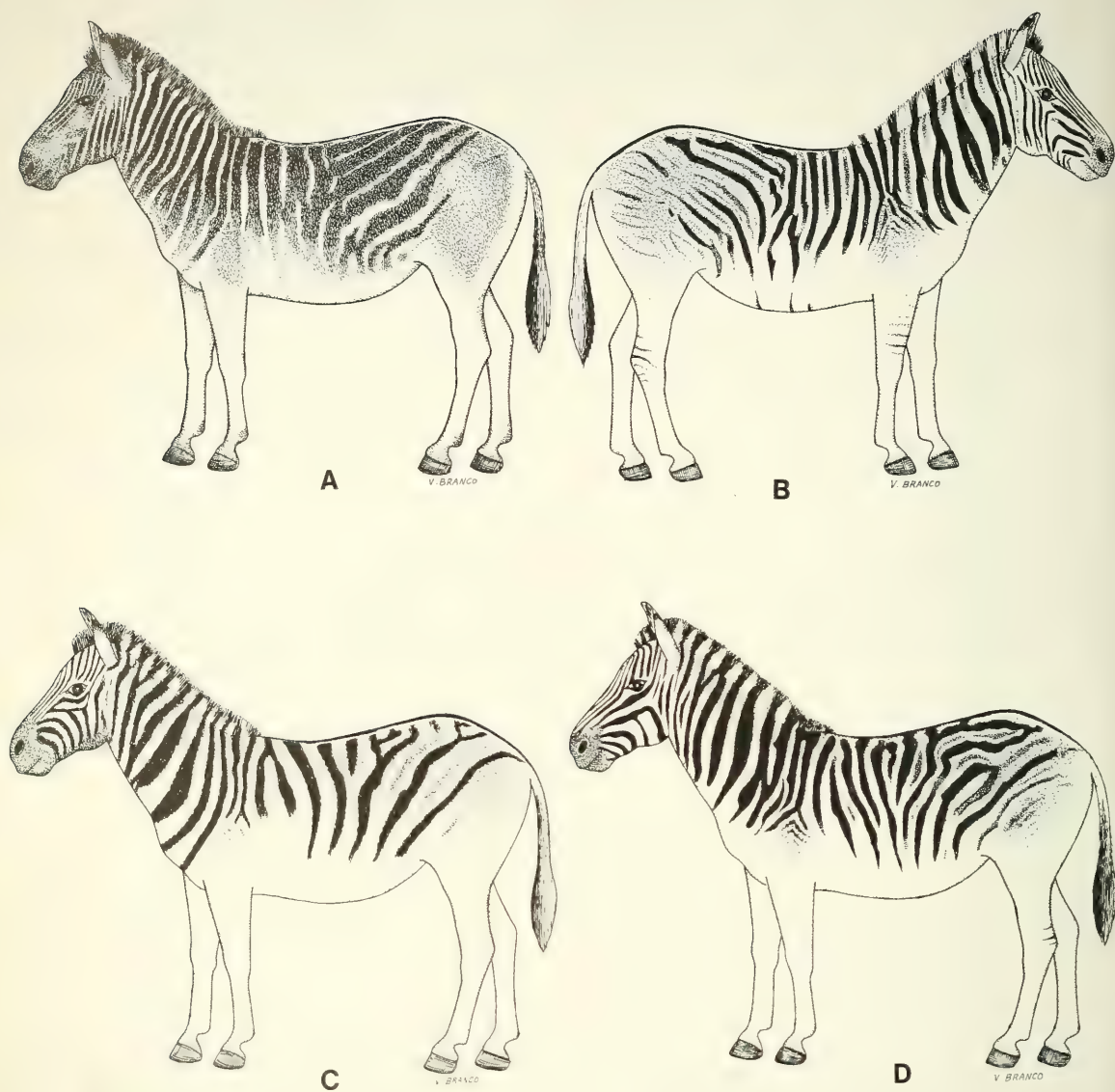


Fig. 9. Stripe patterns and tone of basic colours of various plains zebras, shown in standardized outline. A. Female quagga at Mainz Museum. B. Burchell's zebra from Zululand (same as Fig. 7B). C. Male Burchell's zebra at Leiden Museum. D. Burchell's zebra from Zululand (same as Fig. 7D). E. Quagga at Tring Museum (near London). F. Type of true Burchell's zebra, British Museum (Natural History) (destroyed). G. Quagga at Berlin Museum. H. Male quagga at Mainz Museum. I. Burchell's zebra at Mainz Museum (type of '*Equus burchelli paucistriatus*' Hilzheimer, 1912).



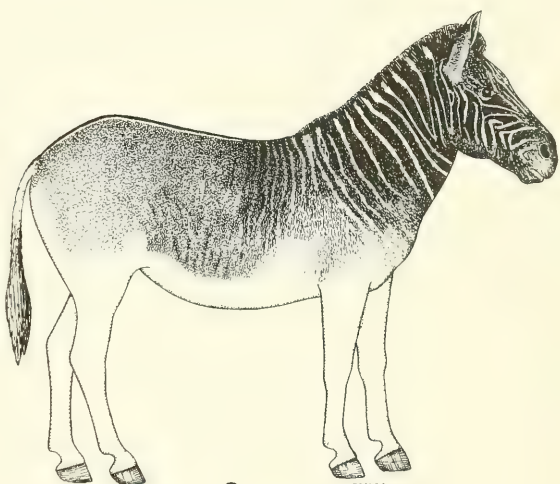
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Both plains and mountain zebras are amongst those South African mammals whose ranges have been much restricted during the past three centuries. Now, and in the recent past, zebras are being translocated from areas where populations survive to areas which they formerly inhabited. In the case of the plains zebras such reintroductions have involved the movement into certain areas of forms dissimilar to those which previously occurred there, even though the original form, or one close to it, still exists.

As indicated above, the 'subspecies', *Equus quagga burchelli*, apparently survives in Zululand and thus, when reintroductions of zebras into the former range of the true Burchell's zebra are contemplated, it would be desirable that selected specimens from Zululand be used, rather than animals of the *antiquorum* type. It would even be desirable to eliminate former indiscriminate reintroductions and to replace them with individuals which are closer to the original population. With a minimum of initial selective breeding in order to eradicate recessive *antiquorum* characteristics, which are present also in *burchelli*-like individuals from Zululand (an intergradational area between the two forms), a 'pure' population of plains zebras resembling the former endemics could be achieved within a relatively short period.

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